Pharmacology

The effects of pitressin and pitocin (extracts of the posterior lobe of the pituitary gland) on blood pressure, have been studied in a wide range of vertebrate species. Both drugs affect blood pressure in all non-mammalian species that have been tested, although the effects of each varies in different species. The platypus, a prototherian mammal, also shows blood pressure changes with both drugs. No eutherian mammal has been shown to exhibit a blood pressure response to pitocin, while pitressin causes a rise in blood pressure in these animals. Similar responses to those of the Eutheria have been demonstrated in the only two marsupials—one being the quokka—that have been tested. That this is true for the quokka was first shown by Feakes and Waring (unpublished data) and was later verified by Woolley (unpublished data).

These effects are of interest in relation to the phenomenon of tachyphylaxis (or reduction of response to a drug when serial doses of the same amount are given over a period of time), which has been demonstrated by the above workers in relation to the effects of pitressin on blood pressure in the quokka. Woolley is at present investigating the mechanism by which this tolerance is brought about.

In summary, it can be said that these investigations on the quokka are of great interest in relation to comparative physiology, since relatively little is known of physiological function in the marsupial group. Several unusual mechanisms have been demonstrated and it is possible that some, at least, of these will prove to be characteristic of the macropod group.

S. BARKER and J. BARKER.

15.—Rottnest Field Studies Concerned with the Quokka

Rottnest Island is a study area of value to field ecologists interested in the dynamics of mammal populations. It is closed to recruitment by immigration and to loss by emigration such as occurs in continental populations in response to climatic or seasonal change.

Its area is 4,700 acres, i.e., not so small as to make it an extremely artificial study area. The single species of indigenous mammal, the quokka, is a herbivore with no carnivorous predator so that no complication in the way of predator-prey relationship obscures the direct relationship of the animals to the environment. The animals are small (adult: 3.5kg), easily caught, and relatively docile when handled. In captivity they domesticate easily for experimental work. Practically all the females have one young per year, there being no observable senescence in the population. Although accounts of the early days of the colony indicate that large numbers of the animals were shot for sport prior to 1914, since that date the Island has become a game reserve and with complete protection the population has become virtually a natural population with human checks removed. All these factors add up to the fact that this Island and its indigenous quokka population provide a relatively simple ecological situation. When it is realised that the search for such situations has in recent years driven ecologists to the simplified regions of the desert, tundra and the steppes, it is fortunate that we have so close at hand in Western Australia a study area capable of producing a growing body of fundamental research on a marsupial population.

One of the fundamental questions of population dynamics concerns the limiting factors of population growth. Starvation and disease are the causes most favoured by mammalogists. Prolonged seasonal adversity in the form of drought in hot deserts and blizzards in cold deserts decimates populations seasonally or periodically. Less frequently it can be demonstrated that the fertility itself is affected by adverse conditions of food, water or disease and this adjusts population numbers without the spectacular death rate associated with the three major limiting factors.

Since the original landing of Volckersen 300 years ago the journals of the various navigators and naturalists indicate that the population of the Rottnest Island quokka was dense enough to elicit comment. Today the quokka numbers are still large. The Island has been separated from the mainland some 7,000 years according to Churchill (1959) and one can speculate that over the major part of this period the density of the animals has been high.

What then are the natural limiting factors of this population? Initially an attempt was made to establish some correlation of death with season. If successful this would give a clue to the probable cause. As no recently dead or moribund animals are in evidence at any season no pathological evidence can be sought to give a lead to the immediate cause of death. In fact animals in this condition are rarely found, as the sick animals presumably seek shelter before becoming moribund and die unnoticed until destruction of the vegetation reveals their skeletons. These are common on the Island. Hence, as the only remaining evidence of natural deaths, a large (600) collection of crania was made in the hope that they would reveal some seasonal pattern of death. It seemed upon analysis that the major part, if not the whole of the population deaths, takes place in the late summer, i.e., March and April. This observation gave a valuable lead because any limiting factor had to be operative at or a little before this period.

With an established season of death further analysis of such a population could proceed on two parallel lines. Either the biotic environment of the herbivore could be studied for the effect of grazing, or the population of animals themselves could be studied by extended sampling, the knowledge of their clinical status providing an assessment of the factors contributing to morbidity. Both these lines of attack have been and are still carried on with the Rottnest Island quokka population. Initially the latter approach was used—an analysis of the physiological status of the population through a complete haematological survey extending over some two years, with large samples of animals, repeated periodically throughout the year. We knew that semi-starvation in general produced an anaemia and that this anaemia was probably of a special type—hyperchromic and macrocytic. Summer dehydration, acute or chronic was expected to produce the reverse picture—a haemoconcentration. Generalised disease has its own general indicators in raised white cell concentrations and high sedimentation rates of red cells whilst the evaluation of vitamin B_{12} deficiency is most easily determined by blood serum bioassay. B_{12} deficiency has not been demonstrated in animals other than the sheep, but seemed a possible limiting factor in this case.

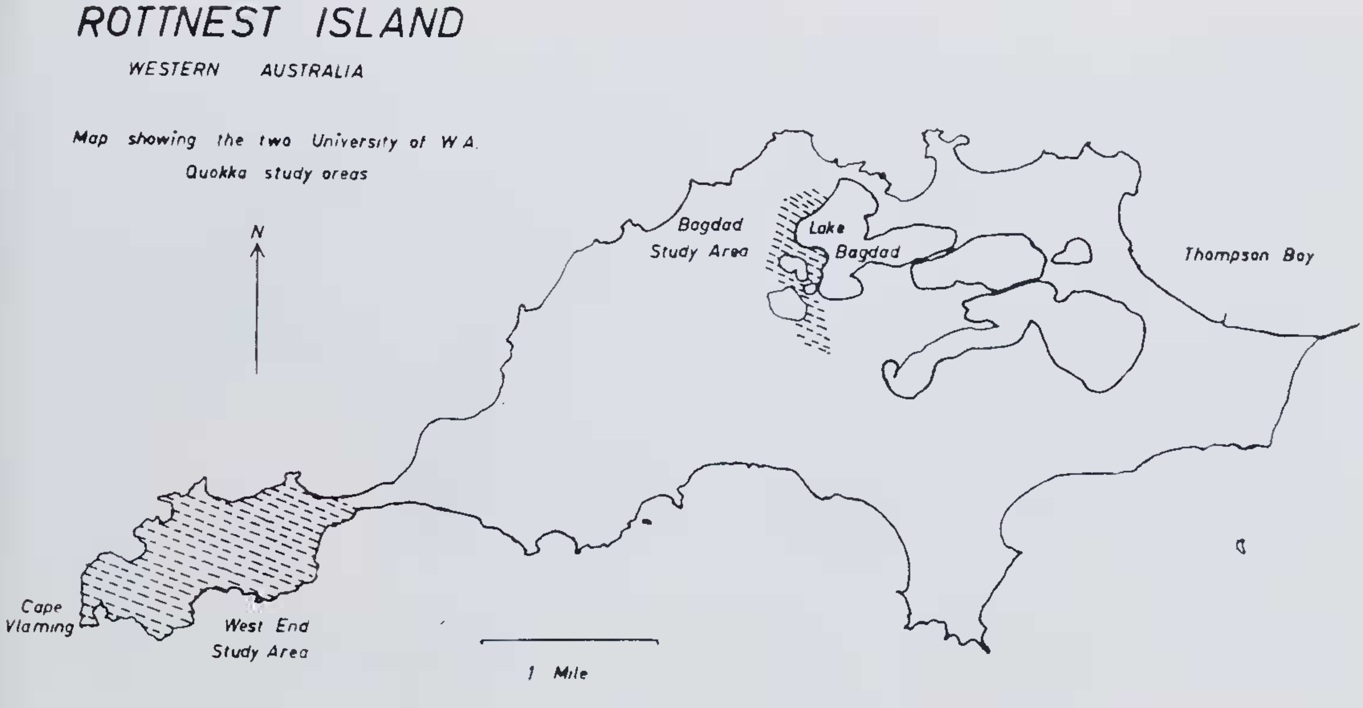
Two study areas have been selected on the Island—one comprising the whole of the west end of the Island; an area of some 500 acres joined to the main island by a narrow isthmus, whilst the other is located adjacent to Lakes Bagdad and Pink and totals in all about 300 acres.

The West End study area contains no free fresh water and the animals presumably satisfy their water requirements from that contained in their food. The other study area—Bagdad—has an ample water supply all the year around as a number of seepages around the periphery of the salt lakes flow summer and winter. To use two areas so dissimilar in their available drinking water for a physiological evaluation of the animals in each could show whether dehydration operated as a limiting factor on the West End animals during the summer, when the mortality pattern appeared constant all over the Island on the evidence of the skull collections. Thus similarity of mortality incidence in West End and Bagdad could suggest that the lack of potable water on West End was not a contributory cause there. However, it is a well known phenomenom that thirsty animals will not eat, so that chronic water shortage leads to starvation which, rather than dehydration, then becomes the proximal cause of death. With this thought in mind the similarity of the seasonal pattern of death in the two study areas may relate to different causes, that of the West End being primarily mediated by dehydration. Inanition due to food shortage in the presence of water and inanition due initially to chronic water restriction, but a really secondary starvation, present clearly separable blood pictures.

The necessary experimental evidence came from a colony of quokkas kept in the zoology yards which had been subjected to water restriction for a period of 6 or 7 months. The *chronic* dehydration of the experimental animals produced, after some months of continued water restriction, a blood picture which differed both from acute dehydration and primary starvation: on the one hand an anaemia in so far as the haemoglobin and red cell concentrations fell below the average of the control sample as did the haematocrit values, and on the other, an increase of the serum proteins, both albumin and globulin, over those values in the control animals which were maintained on a diet of food and water *ad. lib.*

In the field under summer conditions the blood picture was the same for both areas, giving no evidence that either acute or chronic dehydration supervened in the West End despite the total lack of free fresh water.

With the demonstration by Moir, Summers and Waring (1956) that the quokka was ruminant-like, possessing a large stomach, and an oesophagael groove very like that in the sheep the question arose as to whether low cobalt



values which had previously prevented the establishment of sheep at Rottnest, also affected the macropod population; in particular could this act as a specific limiting factor to population growth? Experimental work with sheep had demonstrated that a drop in serum B_{12} values paralleled a progressively developing "coast disease," overt symptoms of the disease appearing at a definite low level of the serum vitamin concentration in the experimental animals. For this reason it was thought that a haematological survey of the quokka population over a complete season would reveal any deficiency comparable to that in sheep. We were fortunate in having the haematology department of the Royal Perth Hospital able to do all our B_{12} assays. The survey was conducted during 1956-57 and over the whole period for both study areas a total of some 450 animals were assayed. At no season did the Rottnest average B_{12} values fall as low as those in "coasty" sheep. Instead a seasonal variation in the quokka B_{12} level was evident such that the maximum occurs in the late summer, not the minimum which would be expected to correspond to the mortality peak. In addition statistical analysis revealed no correlation with haemoglobin or albumin levels with low B_{12} levels as in the case of experimental animals. Hence, taken together, the several aspects revealed by the serum B_{12} assay indicates that the soil cobalt deficiency (low enough to totally eliminate a eutherian ruminant, the sheep, from the area) does not affect its marsupial analogue, the quokka.

The extreme control of the Island's vegetation by the quokka has been demonstrated in several ways. In February 1955 fires burnt out the whole middle of the Island. Immediately afterwards the Zoology Department erected 25 animal exclusion quadrats on various burnt areas. After two years of subsequent regrowth the effect of the quokka grazing was amply demonstrated by the luxuriant growth inside a majority of the quadrats and the poverty outside. The immediate implication of this was that the animal population itself was being primarily controlled by starvation. Semi-starvation uncomplicated by disease has a fairly definite blood picture (Keys, Brozeck, Henschel, Michelson and Taylor, 1950). There is a rather profound anaemia of the order of 25 per cent. decrease in the haemoglobin, red cell count, and haematocrit. This anaemia is generally of the macrocytic, hyperchromic type. (Over a period of some two years the seasonal anaemia of the quokka during late summer has been of this type, the blood picture corresponding to what the World Health Organization (1951) regards for humans at least as a severe semi-starvation anaemia.) However, these figures are averages. Hence 50 per cent. of the population will be below this value and some smaller percentage will be in the pathological range of blood values indicative of severe starvation. Parallel to the decrease in formed elements of the blood was a decrease in plasma proteins, with this effect more marked in the albumin rather than the globulin fraction.

All the foregoing considerations taken together suggest that it is most probable that semi-starvation is the condition of the general Island population with starvation the fate for some proportion each year, as evidenced by the skull data.

Starvation in mammal populations is rarely unaccompanied by disease when population numbers are high. As previously mentioned no moribund animals were available for their pathology to be determined and so other measures of disease were required. White blood cell concentrations and the sedimentation rate of red cells are general non-specific indicators of disease. True, both these measures are affected by conditions other than disease, e.g., diet and pregnancy, but in general large variation in sedimentation rates indicate tissue destruction, whilst an increase in white cells indicates active increase in phagocytosis. As a result of the survey, cycles were found also in these two blood measures. However, the trends were the opposite to expectation on an hypothesis of seasonal disease in the late summer. The white cell counts on the average fell to low values during this period—this being expected in starvation. Similarly low sedimentation rate values were found in the summer, this probably reflecting the decrease in plasma proteins, which correlation is known to exist.

Rectal temperatures of all animals captured also follow a seasonal trend when plotted. An average drop of some 2.5°C. for the West End animals occurs in the late summer as compared to winter values. A control colony well fed and watered on the mainland shows no comparative drop during the summer. Studies on domestic ruminants have shown that the heat of fermentation as measured by body temperature rise is appreciable after a meal. The quokka being ruminant-like will have a digestion which will also contribute this heat of fermentation to its general metabolic heat. The relatively large drop in rectal temperature at the summer season possibly reflects the starvation, being the combined effect of recession of fermentation and the lowering of the metabolic rate consequent upon starvation.

From this field survey it is seen that positive indications exist only for starvation as the controlling factor of population increase for the Rottnest Island quokka (and see report on the Physiology of the Quokka in this part). Other factors either have contra-indications or no evidence can be adduced for their effect. These indications are over the study-years of 1955 through 1958, but no unusual seasonal or other conditions which could make the study-years non-representative have been discovered.

J. W. SHIELD.

References

Keys, A., Brozeck, J., Henschel, A., Michelsen, O., and Taylor, H. (1950).—"The Biology of Human Starvation" (Univ. Minnesota Press: Minneapolis, Minn.)

Joint F.A.O./W.H.O. Expert Committee on Nutrition (1951).—Prevention and treatment of malnutrition in times of disaster. World Health Organization Technical Report Series No. 45. World Health Organization, Geneva 21.

Fig. 1.—Exclosure in *Acacia* thicket burnt February, 1955, north of Biological Station. Strong regrowth of *Acacia* inside fence hides other species not seen outside. *Stipa* and *Thomasia* clumps in foreground.
Photograph, J. W. Shield

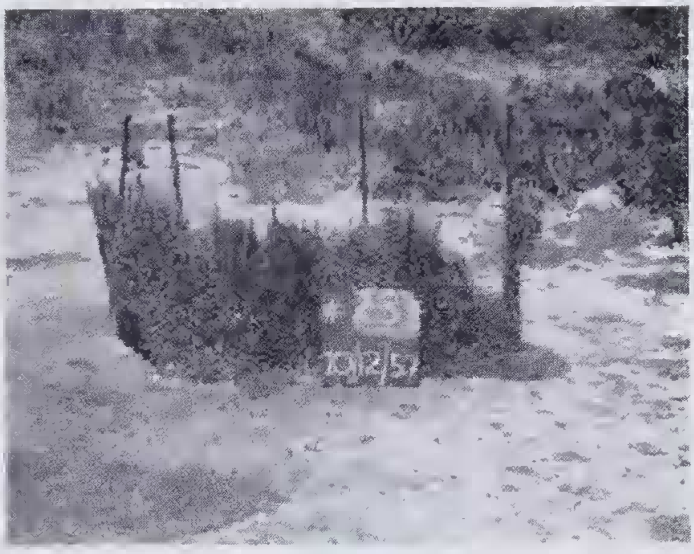


Fig. 2.—Exclosure at Barker's swamp. Note the dense regrowth of halophytes inside the fence. *Suaeda* is abundant inside the fence but rare outside.
Photograph, J. W. Shield

Fig. 3.—Quokka. Flashlight photograph of young adult.

Photograph, A. R. Main

Fig. 4.—Wilson Bay. Wide intertidal platform with outer part terraced. Small intertidal undercut. Note cross bedding in aeolianite rock.
Photograph, E. P. Hodgkin

Fig. 5.—Fish Hook Bay. Photograph taken through deep intertidal undercut at entrance to bay. Low tide. Pole height six feet.
Photograph, E. P. Hodgkin

1955, in centre of island between lakes and [illegible] neck.
Photograph by courtesy of West Australian Newspapers Ltd.

Photograph, A. R. Main, April, 1954

Fig. 8.—Central part of Rottnest Island, looking west. April, 1954. Shows vegetation before the 1955 fire. Arrow points to Biological Station.
Photograph, A. R. Main

Fig. 9.—Aerial photograph shows upper Serpentine and part of main Serpentine lakes. Note seepage area (top and right of upper lake, *Gahnia* clumps adjacent to these, *Melaleuca* copse in foreground, *Acacia* top left, *Tuart* plantation top right.
Photograph, A. R. Main